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Return of the Giants

Restoring Western White Pine to the Inland Northwest

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ABSTRACT

Relatively high levels of blister rust infection in some stands of genetically improved western white pine *(Pinus monticola)* raised concerns that resistance may fail under field conditions. However, surveys show consistently lower infection and mortality in genetically improved white pine compared to unimproved stock. Restoring white pine by continued breeding for high levels of rust resistance, increased planting of resistant seedlings, and other silvicultural treatments are recommended to help alleviate forest health problems in Inland Northwest forests.

Keywords: blister rust; forest health; pathology

In the late 19th century, western white pine *(Pinus monticola)* dominated the moist, mid-elevation, mixed-species forests of the Inland Northwest. This single species represented 45 to 55 percent of the volume of second-growth and mature stands in the region, with old-growth stands sometimes exceeding 100 mbf per acre (Haig et al. 1941; Neuenschwander et al. 1999). By the 1920s, white pine had become the mainstay of the Inland Northwest's forest industry, averaging 430 mmbf cut annually between 1925 and 1934 (Haig et al. 1941). White pine lumber production was particularly important in northern Idaho, where the annual cut ranged from 190 to 466 mmbf between 1925 and 1938 (Hutchinson and Winters 1942).

But by the late 1960s, the combined effects of high-grading, overcutting, mountain pine beetles, reduction in stand-replacing fires, and blister rust

Above: **In 1937, this 160-year-old stand at Montford Creek Natural Area in the Deception Creek Experimental Forest was an excellent example of the white pine forest type. By the time the stand had reached 200 years, beetles had killed nearly all the white pines.**

had decimated the once-majestic white pine forests of the Inland Northwest. Of all the factors, blister rust, against which American white pines have little natural defense, was the most damaging.

Less than 10 percent of the historic 5 million acres of white pine cover type remains in today's Inland Northwest forests (Fins et al. 2001). White pines, which require near full sunlight to maintain rapid growth, have largely been replaced by more shade-tolerant species, such as Douglas-fir *(Pseudotsuga menziesii),* grand fir *(Abies grandis),* and western hemlock *(Tsuga heterophylla)* (O'Laughlin et al. 1993). But these new forests are more disturbance-prone and less productive than historic white pine stands. Furthermore, where white pine forests commonly produced 50 mbf per acre, the best mixed-fir stands of today average only half that much (Mahoney 2000).

Can the decline of Inland Northwest ecosystems be reversed? If so, the crux of the change will likely be found in silvicultural practices that emphasize widespread planting of rust-resistant white pine seedlings and the creation of large forest openings where the pines can outgrow competing shade-tolerant species. Only an aggressive, coordinated silvicultural approach will promote a healthier, more resilient forest and a "return of the giants."

Blister Rust in Context

White pine blister rust was inadvertently introduced into both eastern and western North America on infected nursery stock imported from Europe around the turn of the 20th century (Mielke 1943). By 1923, some of Idaho's western white pines were infected; by the 1940s the infection was epidemic throughout the Inland Northwest (Bingham 1983).

Cronartium ribicola is the fungus that causes blister rust. This pathogen has a complicated life cycle that includes five spore stages and requires two hosts—*Ribes* species (gooseberries and currants) and white pines—to complete its life cycle. During spring, bright orange spores that are shed from "blisters" on infected white pines infect the leaves of *Ribes* plants. Over the summer, the rust progresses through several spore stages, intensifying the infection on the *Ribes* plants. Then, with the lower temperatures and higher moisture levels of fall, the rust completes its life cycle, infecting white pines with wind-dispersed spores produced on the underside of infected *Ribes* leaves.

Blister rust infects the pines when germ tubes of germinated rust spores enter the tree's needles through their stomata (Mielke 1943). The fungus grows into the needles and branches and down into the main stem, producing stem-girdling cankers in susceptible trees. The cankers eventually kill the trees or their tops, depending on their height on the tree's bole. Although small trees usually succumb quickly, large trees can live for many years before the infection causes obvious damage (Moss and Wellner 1953).

Starting in 1909, the USDA Forest Service and forest industry made valiant efforts to save white pines by attempting to interrupt the life cycle of the fungus. They tried numerous tactics, including efforts to eliminate *Ribes* plants from white pine ecosystems and injecting antibiotics directly into the bark of infected trees (Ketcham et al. 1968). Approximately $150 million was spent over a period of about 50 years in efforts to control blister rust (Maloy 1997). But none of the programs was able to stem the advance of the rust. After a 1966 survey of the effectiveness of the various tactics, the *Ribes* eradication program was discontinued, the antibiotics program was severely curtailed, and the harvest of merchantable white pines was accelerated (Ketcham et al. 1968).

Genetic Resistance

Meanwhile, in the 1950s, R.T. Bingham and his colleagues J.W. Duffield and A.E. Squillace demonstrated genetic control of blister rust resistance in selected white pines from heavily infected natural stands in the Inland Northwest, primarily northern Idaho (Bingham 1983). In 1957, using the most resistant seedlings from matings among approximately 40 candidate parent trees, Bingham and his colleagues planted the first trees in a new breeding orchard in Moscow, Idaho. Between 1971 and 1974, the USDA Forest Service established three seed orchards using selected progeny from 72 of the original 400 candidate trees. When a sufficient number of trees became reproductive, a second generation of progeny (the F_2 generation) was produced from controlled matings between trees in the breeding orchard. In a classic study that is still cited frequently, 66 percent of the F_2 seedlings were found to have no cankers at 2½ years after inoculation with a high number of *C. ribicola* spores (Hoff et al. 1973).

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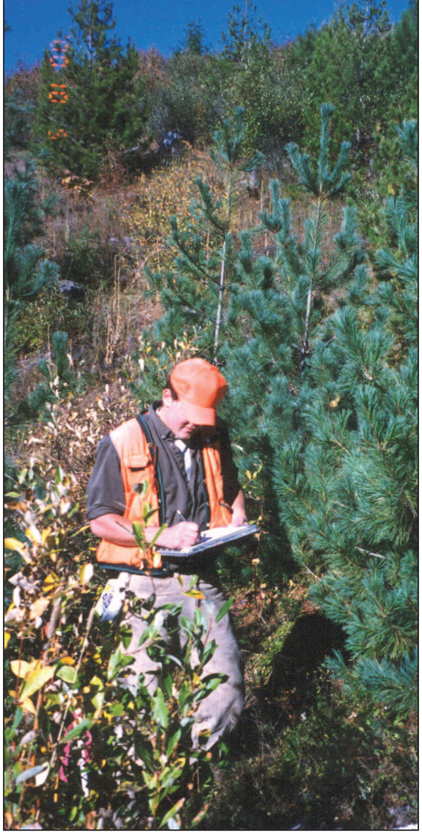
Blister rust spores invade white pine trees through stomata on the needles. In susceptible trees, the fungus eventually grows into the bole of the tree, causing a girdling canker.

The breeding orchard began to produce small seed crops around 1970, and the site was converted to a seed orchard in the 1980s. To date, the Moscow seed orchard has produced approximately 10,000 pounds of seed, and Forest Service seed orchards have produced nearly 4,000 pounds, about 280 million seeds in total (Fins et al. 2001; Eramian 2002, pers. commun.). Estimated rust-resistance levels from these and other regional seed orchards range from 35 percent to 80 percent and generally include a broader genetic base than the orchard at Moscow.



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Studies of field-planted white pines show significantly lower levels of infection and higher survival in the rust-resistant trees compared with woods run stock.

Despite the large amount of rust-resistant seed produced, only about 5 percent of the estimated 5 million acres in the Inland Northwest that are suited to growing white pine has been planted with rust-resistant stock. In fact, treeplanting has declined in recent years as timber harvests have been decreased on public lands (Neuenschwander et al. 1999).

It might be argued that natural selection and natural regeneration will eventually restore white pine to Inland Northwest ecosystems. Indeed, natural selection has begun to increase rust-resistance levels in some naturally regenerated stands that have been challenged repeatedly by blister rust (Meagher and Hunt 1996). These stands represent reservoirs of genetic diversity that may be important to the long-term survival of the species, as do the few remaining mature white pines that can occasionally be found in protected areas. But most of the white pines in young naturally regenerated stands are killed by blister rust. The old veterans also continue to succumb to blister rust and bark beetles, and they are at high risk of loss to wildfire due to the buildup of forest fuels after nearly 100 years of fire suppression (Atkins et al. 1999). Ultimately, the natural processes that could potentially restore white pine to these ecosystems would likely be slow and the results uncertain, leaving many gaps where seed sources are already missing or where openings are inadequate for white pine regeneration.

Evaluating Resistance under Field Conditions

The clear alternative for restoring white pine to Inland Northwest ecosystems is to continue planting genetically improved, rust-resistant white pines. One potential caveat is that, to date, the long-term stability of rust resistance in the improved stock has not been fully determined. However, a few plantings were established with assessment of long-term performance as their primary objective (Bingham 1983), and it is also possible to use field plantings for this purpose. Thus, between 1992 and 1997, levels of infection and mortality from blister rust were assessed in four genetic tests, six paired (side-by-side) operational field plantings of F_2 and unimproved stock, and 14 operational plantings of F_2 stock alone (unpaired). The objectives of the evaluations were to assess variation in rust incidence across a wide variety of sites and to compare the performance of genetically improved stock to that of unimproved stock under field conditions.

In genetic tests, tree identities are known, their planting locations are mapped, and the tests are inspected at regular intervals. These tests thus provide excellent opportunities to monitor not only the occurrence but also the progression of blister rust infections (McDonald and Dekker-Robertson 1998). Paired operational plantings provide good opportunities to compare the performance of genetically improved and unimproved stocks growing under similar operational reforestation conditions, while the operational plantings of the F_2 stock provide a broad measure of the stock's performance across a wide array of environmental conditions.

With the exception of the genetic tests, field assessments were conducted using nonpermanent plots along transects through the plantations. Paired *t* tests were used to compare infection and mortality levels of improved and unimproved stock at sites where both were planted. Because the surveys could not detect early mortality due to rust or other causes in the operational plantings, the baseline for the reported levels of infection is not the number of trees that were planted but rather the number of trees that were present at the time of the survey.

Table 1. Infection levels in 14 planted stands of F_2 western white pine in northern Idaho, 1997.

Site	Years since planting	*N*	Percent infected
Priest Lake 1	8	83	2.5%
Priest Lake 2	8	40	12.5
Palouse 1	8	129	33.3
Powell 1	9	152	21.1
Powell 2	9	109	35.8
Pierce 1	9	104	26.9
Pierce 2	9	116	32.8
Lochsa	9	112	64.3
North Fork 1	10	107	15.9
Palouse 2	11	99	19.2
North Fork 2	12	172	20.9
Fernan 1	13	69	63.8
Fernan 2	13	105	33.3
Avery	13	88	35.2
Mean		106.1	29.8

NOTES: Surveys were conducted using nonpermanent plots. Overall mortality was not assessed. F_2 refers to seedlings produced from matings between the selected progeny of crosses between the original wild parent trees for the blister rust resistance program.

Table 2. Rust infection and mortality in six Potlatch Corporation operational field plantings of western white pine, surveys conducted 1992–96.

Site	Stock type*	Years since planting	N	Percent infected	Percent killed by rust
French Creek	Moscow improved (F_2)	11	489	48%	13%
	Unimproved	11	379	100	77
Camp 43	Moscow improved (F_2)	11	435	38	9
	Unimproved	11	272	67	52
Robinson Creek 6	Moscow improved (F_2)	12	556	26	5
	Unimproved	12	664	100	38
Robinson Creek 9	Moscow improved (F_2)	11	400	9	0
	Unimproved	11	500	43	12
Scofield	Moscow improved (F_2)	15	150	64	16
	Unimproved	15	137	96	68
West Fork Strychnine	Moscow improved (F_2)	14	150	2	0
	Unimproved	14	150	14	3
Mean	Moscow improved (F_2)		363	31	7
	Unimproved		350	70	42
Mean difference between Moscow F_2 and unimproved				39	35

*F_2 refers to seedlings produced from matings between the selected progeny of crosses between the original wild parent trees selected for the blister rust resistance program.

Notes: Data from these surveys came from nonpermanent plots in six planted stands that contained separate blocks of Moscow F_2 (blister rust resistant) and unimproved western white pine seedlings. All six stands were surveyed first by the Potlatch Corporation. The Scofield and Strychnine stands were resurveyed several years later by the Inland Empire Tree Improvement Cooperative's White Pine Species Group. (Data on file with the Inland Empire Tree Improvement Cooperative, University of Idaho.)

Encouraging Results

The evaluations show three important trends. First, infection levels vary widely across the landscape, even when comparisons are restricted to the same genetic stock *(tables 1–3)*. Of the 24 plantations surveyed, approximately two-thirds (17 of 24) had low to moderate incidence of rust infection (0–38 percent) in the F_2 stock. These percentages are close to or less than the 34 percent infection reported for nursery-tested F_2 seedlings inoculated once with large numbers of rust spores (Hoff et al. 1973). Infection levels in the F_2 stock were relatively high (48–93 percent) in seven of the 24 plantations, approximately 30 percent.

Second, the F_2 stock had consistently and significantly less rust infection than the unimproved stock, with 31 versus 70 percent in the operational field plantings (p = 0.003) and 60 versus 95 percent in the genetic tests (p = 0.04) *(tables 2 and 3, respectively)*.

Third, mortality from blister rust was consistently and significantly lower in genetically improved F_2 white pines compared to unimproved stock in both the operational field plantings (7 versus 42 percent, p = 0.008) and in the genetic tests (25 versus 67 percent, p = 0.01). Even at the Merry Creek site, where the highest infection levels in F_2 stock (93 percent) were observed, 34 percent of the genetically improved F_2 trees were still alive at age 26, while all of the unimproved stock had died by age 12 *(table 3)*. Furthermore, although most of the surviving F_2 trees had rust infections, they were growing well and many were already of merchantable size. Similarly, at the Gletty Creek study site, where the same genetic sources were planted as at Merry Creek, only 13 percent of the genetically improved F_2 stock had died by age 25, compared to 70 percent mortality in the unimproved stock.

The overall results of these evaluations are encouraging. Up to a quarter-century after planting, genetically improved stock has maintained superiority over unimproved stock across a wide variety of environmental conditions. Nonetheless, the relatively high incidence of rust infection in about 30 percent of the F_2 plantings is troubling and provides support for routine monitoring of plantations for sudden changes in infection levels or mortality that may require immediate silvicultural treatments.

A New Strain of Rust?

The incidence of relatively high levels of rust infection in resistant trees raises obvious concerns that the rust may have mutated or otherwise increased in virulence. Mutation is always a possibility, and virulent strains of rust have been found in California and Oregon. But both new strains appear to be ecologically restricted and have not spread beyond very limited geographic areas (Kinloch 2000).

Had virulence in blister rust increased dramatically in the Inland Northwest, the change would likely have been detected in annual screenings of seedlings for rust resistance. Over the past 10 years or so, wild rust spores have been collected from many areas, including the highly infected Merry Creek site. The spores were used to challenge white pine seedlings in rust screening nursery tests, which included check-lots of seedlings with known levels of resistance. If new, virulent strains of rust had been present, the levels of infection in the check-lots would have increased sharply com-

Table 3. Rust infection and mortality of western white pine in four genetic field tests, 1996.

Site	Stock type*	Years since planting	*N*	Percent infected	Percent killed by rust
Jackson Mountain	Moscow improved (F_2)	14	142	60%	11%
	Unimproved	14	132	98	69
New Scofield	Moscow improved (F_2)	14	124	68	10
	Unimproved	14	127	91	29
Gletty Creek	Moscow improved (F_2)	25	163	20	13
	Unimproved	25	216	91	70
Merry Creek	Moscow improved (F_2)	26	104	93	66
	Unimproved	12	171	100	100
Mean	Moscow improved (F_2)		133	60	25
	Unimproved		162	95	67
Mean difference between Moscow F_2 and unimproved				35	42

F_2 refers to seedlings produced from matings between the selected progeny of crosses between the original wild parent trees selected for the blister rust resistance program.

NOTES: The Jackson Mountain and New Scofield tests belong to the Potlatch Corporation. Rust surveys were conducted in these tests in 1996 by the Inland Empire Tree Improvement Cooperative's White Pine Species Group. The Gletty Creek and Merry Creek sites are USDA Forest Service tests.

pared with previous inoculations. However, levels of infection showed no dramatic changes during this period (Mahalovich 1997, 1999, unpublished data). Similarly, if a new, virulent strain of rust had developed at Merry Creek, infection levels at the site also would have increased dramatically in a short period of time. But the long-term records show no such pattern (McDonald and Dekker-Robertson 1998). Thus, at least to date, there is no evidence of a mutant, more-virulent strain of rust in the Inland Northwest.

With no evidence of new strains of rust, researchers have begun to evaluate environmental factors that may promote or hinder infection. Some of the variables that are thought to affect incidence and intensity of rust infection are the proximity of *Ribes* species and their numbers, specific location of the planting (e.g., elevation, aspect, and slope), local climate, fire history, soil conditions, availability of soil nutrients, and physiological conditions of the rust and the trees. A better understanding of the effects of these factors and their interactions will provide a basis for rating sites for risk of infection and probability of success in establishing and supporting new stands of planted white pine.

Progress toward Greater Resistance

The white pine breeding program in the Inland Northwest is designed to increase rust resistance beyond current levels. But genetic immunity, i.e., resistance that prevents an organism from becoming infected, is not a goal of the program. Breeding for immunity has been used very effectively with annual agricultural crops, such as wheat and corn (Simmonds 1991) and may be possible with forest trees. But immunity is usually controlled by only one or a few genes and is easily overcome by mutations in the disease organism. Furthermore, strategies based on immunity require repeated introductions of new resistance genes into a breeding program to stay ahead of mutations in the disease organisms. Because trees are long-lived, it is more prudent to emphasize long-term stability of disease resistance by selecting for multiple resistance mechanisms, at least some of which are controlled by multiple genes.

To be selected for the USDA Forest Service/Inland Empire Tree Improvement Cooperative breeding program, each seedling must exhibit at least two types of rust resistance in nursery trials. It must first belong to a family (e.g., seedlings from the same mother tree are a family) that displays a multigene, or horizontal, type of resistance. Second, it must display a type of resistance thought to be controlled by a single gene, or vertical, type of resistance *(table 4).* Furthermore, the seedling must have superior height growth. Selected seedlings are planted or grafted into seed orchards and later may be mated to each other in the breeding program. New orchards are expected to produce progeny with much higher levels of rust resistance than the older orchards.

It should be noted that the genetic strategy used in this program will produce trees that can become infected with blister rust. The disease will, in fact, kill some of the trees. However, most of the trees produced, even if they become infected, are expected to survive the infections and continue to grow, perhaps for centuries.

Management Implications

The high levels of rust in some of the plantations surveyed underscore both the need to anticipate conditions that promote rust infection and the need to routinely inspect existing plantations for rust incidence. With knowledge of the conditions that promote rust infection, high-risk sites can be avoided or planting densities may be increased to compensate for anticipated losses. Routine inspections will allow the use of silvicultural treatments that can enhance the performance of white pines already on site and minimize their loss to the disease.

Any actions taken should reflect management objectives for an area. Nonetheless, when regenerating stands, it is prudent to leave the best residuals on site. These survivors can

Table 4. Selection for rust-resistance traits in western white pine.

Type of selection	Resistance category	Resistance trait*	Description
Family	Horizontal (multigene)	Low needle lesion frequency	Seedlings have a relatively small number of needle lesions, based on number of spots per meter of needle length.
		Early stem symptoms	Cankers and/or bark reactions take a relatively long time to develop. Selected families exhibit a small number of cankers and/or bark reactions at the second inspection compared to the number at the fourth inspection.
		Canker alive	A high incidence of live seedlings have active cankers at the fourth inspection.
		Bark reaction	High proportion of bark reaction in cankered seedlings at the fourth inspection.
Individuals within families	Vertical (single-gene)	No spots	Seedlings appear to be immune to rust infection. No lesions form on the needles after inoculation with rust spores.
		Needle shed	Seedlings develop needle lesions after inoculation with rust spores but drop the infected needles the first summer after infection.
		Fungicidal short shoot	Seedlings develop needle lesions after inoculation with rust spores, but they retain their infected needles and do not develop a canker.
		Bark reaction	Seedlings develop needle lesions after inoculation with rust spores and they develop a canker, but canker growth is arrested.

**Bark reaction appears to function as both a horizontal and a vertical resistance type. The genetic control of the expression of resistance remains unknown.*

NOTES: Screening for resistance to white pine blister rust is conducted in forest nursery beds. Seedlings are inoculated with rust spores in the fall of their second growing season and are inspected four times over the following three years.

help maintain genetic diversity in white pine populations and allow natural selection to take its course, potentially enhancing resistance levels in naturally regenerated stands.

If higher-than-expected levels of infection are found in plantations, foresters should consider integrated management strategies that might include pruning and thinning to reduce the impact of the disease (Hagle et al.1989; Schwandt et al.1994; Hoff et al. 2001). Treatments such as these will remove current infections and minimize future infections while improving growth and stocking levels of desirable species.

The Future

The results presented here clearly demonstrate higher survival rates in the genetically improved stock compared to unimproved stock, even after 25 years under field conditions. While the first 25 years is no guarantee of centuries-long life for the genetically improved trees, their survival thus far suggests some stability in resistance under annually varying spore loads and inoculation conditions. Nonetheless, the higher-than-expected incidence of rust in about one-third of the plantations and the broad-scale loss of white pine cover type in the region underscore the need to enhance both the breeding program for genetic resistance to rust and the regional planting program.

Research is needed to determine more accurately the number of resistance mechanisms and their genetic control, the physiological processes by which they operate, and their long-term stability under a variety of field conditions. Recent research suggests that differences in needle surface traits may be one of the factors related to differences in infectability of seedlings (Woo et al. 2001). New methods of genetic analysis may help by identifying genetic markers for rust resistance that will shorten the rust screening process and increase its accuracy. But classical selection and breeding will remain at the core of programs designed to generate seeds and other propagules for reforestation.

Critical to management decisions is information on how environmental conditions interact with the rust and its hosts to promote or curtail infection and how cultural treatments such as pruning, thinning, and nutrient management affect long-term survival and the disease process. Answers to some questions will become available as ongoing research studies are completed, but what is also required is a commitment to sustain long-term research, continued breeding, increased planting, and intensified management of stands to favor the species for which the forests of the Inland Northwest were known. Ultimately the legacy of that effort will be forests with towering and healthy white pines that will remain long after this generation of foresters and geneticists has gone.

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